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Suppressive Effect of Sustained Low-Contrast Adaptation followed by Transient High-Contrast on Peripheral Target Detection

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Abstract

We observed that presenting a low-contrast Gabor patch (2cpd, 5deg eccentricity, contrast = 4%) for 8 seconds and then flashing a 20-30ms high-contrast patch over it could elicit the perceptual disappearance of a subsequent low-contrast stimulus, whereas neither low-contrast adaptation nor high-contrast flash alone had any considerable effect ($p < .00001$). In other experiments we found: a) suppressive components are phase-insensitive, b) the effect transfers between eyes, c) suppression is selective for orientation, and d) the induction by the transient high-contrast Gabor patch could be transferred to another previously adapted location up to a few degrees. Results indicate synergy between contrast and adaptation through a non-linear interaction between rapid gain adjustment to transient change and adaptation to sustained spatial patterns. Findings are compatible with non-local mechanisms presumably at the cortical level.

Keywords: contrast and edge adaptation; peripheral visual field; detection; filling-in; Troxler fading; visual transients

1 Introduction

The term “visual disappearance phenomena” groups a spectrum of loosely related circumstances under which salient visual stimuli become perceptually invisible (suppressed). In binocular rivalry, the visual input to each eye is different and one often perceives the input received by one eye alone (Wheatstone, 1838; Blake & Fox, 1974). After a few seconds, the percept may switch to the other eye. In fading of a low-

contrast peripheral target under prolonged strict fixation, suppression follows adaptation rather than rivalry. This phenomenon was described originally in 1804 by Troxler for colored images (Aulhorn & Harms, 1972), and later for low-contrast gray scale images (Cibis, 1948). Troxler fading has been explained in terms of adaptation to the target boundaries (Krauskopf, 1963), followed by filling-in of the target area with the surrounding background pattern. Unlike rivalry, small eye-movements or foveation disrupt Troxler fading.

Recently, visual transients are discovered to trigger disappearance in normal viewing condition. One example is motion-induced blindness (Bonneh, Cooperman & Sagi, 2000), where highly discriminable targets perceptually disappear and reappear for periods of several seconds when a global moving pattern is presented in the background. Another example was found by Kanai & Kamitani (2003), who demonstrated that a local transient signal such as flashing a ring, apparent motion, or even blinking the target is sufficient to trigger the disappearance of a perceptually salient (but near equiluminance with the background) target. Note that these two phenomena are analogues of masking by moving objects (Grindley & Townsend, 1965), and flash suppression (Wolfe, 1984) in binocular rivalry, respectively. Only in normal viewing condition, suppression is not in the context of rivalry between two images. Does the transient signal boost earlier adaptation (instead of rivalry), inducing suppression of the subsequent activity?

Foveation can disrupt motion or transient induced blindness, so local adaptation (similar to Troxler fading) might play a role in the fore-mentioned disappearance phenomena. It is often argued that neither phenomenon requires long steady fixation as opposed to Troxler fading. However, shorter adaptation time can be achieved using high-contrast edge adaptation (Shimojo & Kamitani, 2001). These observations motivated us to reexamine the role of adaptation. More specifically, we investigated if transient high-contrast exposure induces disappearance after adaptation to low-contrast spatial patterns, whether there is any interaction between them, and if so, at what level of visual processing does the interaction occur.

We observed that briefly increasing the contrast of a peripheral low-contrast object after a few seconds of strict fixation elicits disappearance of the object, resulting in perceptual filling-in of the location with the surround (Figure 1a). After a short time usually around one second the object reappears. Hence, following sustained adaptation to a low-contrast target, transient high-contrast stimulation can induce perceptual

disappearance. We refer to this illusion as “induced disappearance,” and will use the term “induction” to refer to the transient high-contrast exposure after sustained adaptation to a low-contrast pattern.

Figure 1 inserted about here

The induced disappearance illusion was equally strong when we inverted the contrast of the high-contrast flash in a subsequent experiment (Figure 1b), or when the target was darker than the background. Therefore, the disappearance of the target can not be explained by light adaptation in retina (see also Experiment 1). We observed that the target reappears after slight eye-movements. Note that eye-movements result in a visual signal only where luminance is not homogenous (first-order edges). Presumably, induced disappearance is mediated by filling-in following suppression of boundaries. However, we failed to induce disappearance using texture defined targets (second-order edges, see Experiment 3). These observations indicate that induced disappearance predominantly suppresses first-order spatial patterns. Therefore, in subsequent experiments we used Gabor patches to study induced disappearance.

The main difference between the present study and previous studies is the assessment of the combined effect of the sustained low-contrast and transient high-contrast stimuli. We replicated and quantified our findings using Gabor targets (Experiment 1). Inter-ocular transfer of the disappearance and orientation selectivity was studied in experiments 2 and 3. In Experiment 4, we showed that the induced disappearance of the target is not local to the site of high-contrast stimulation. Results are discussed in terms of an optimal neural encoder with internal noise.

2 General Methods

Volunteers from the California Institute of Technology with normal or corrected to normal vision participated in one or more experiments (2 authors and 7 (3, 8) naïve observers for experiment 1 (2, 3, respectively), 1 author and 5 naïve observers in experiment 4). Experiment sessions were conducted in a dimly lit room, with the monitor as the only light source. The stimuli were presented on the computer screen (Sony Multiscan 20sh, 1024x768). Participants viewed the screen binocularly from 53 cm and were

asked to keep their gaze at a red crosshair presented at the center of the screen over the homogenous gray background (36cd/m²) during the whole session. After 30 seconds, trials started. Each trial consisted of an adaptation phase, during which a low-contrast Gabor signal (2 cpd, $\sigma = 1.4$ deg, unless otherwise specified in the description of the experiment, contrast $\approx 4\%$) were randomly presented in one quadrant at 5 degrees of eccentricity, followed by a brief (20ms) high-contrast Gabor signal (induction) with similar spatial parameters (unless mentioned otherwise) at the same location. After 50ms, a low-contrast Gabor signal (target) was displayed for one second, followed by a random-dot mask (Figure 2b).

Observers were instructed to press a key to indicate presence or absence of the target stimulus. In about 20 percent of the trials (catch trials), no target was presented. To avoid confusing adapting and target stimuli, the color of the fixation crosshair was temporarily changed to yellow to indicate the test phase of the trial. The next trial started 2 seconds after the response, always in a different quadrant. The phase of the sustained low-contrast Gabor was shifted by $\pi/2$ every 250 milliseconds to reduce the retinal adaptation. In Experiment 1a that we also used stationary Gabor signals during the sustained adaptation phase.

In a preliminary experiment, disappearance was successfully induced in eight naïve observers and the two authors. For three other observers, the frequency of fading was non-selectively too low for a quantitative assessment: the subjects always correctly identified the presence or absence of target in all conditions. However, a result similar to other observers was obtained when we increased the width of the flash ($\sigma = 1.87$ deg) and increased its duration to 30ms (two subjects) or 50 ms (one subject). For these subjects we used the modified parameters in all experiments. Two of these subjects did not participate in data shown in figures 4 and 6 for unrelated reason.

3 Induced disappearance vs. adaptation and masking

3.1 Experiment 1a

Under specific circumstances sustained adaptation can elicit disappearance of a low-contrast target. Prolonged adaptation results in the elevation of the contrast threshold that may be enough to suppress the stimulus (Troxler fading). Similarly, transient exposure to a high contrast stimulus can mask a subsequent

less salient target stimulus, especially when the target is presented for a short duration (forward masking effect). Adaptation and masking are conceived to involve different circuitries. Is the observed disappearance of the target after sustained adaptation to low-contrast and induction with transient high-contrast a separate effect? Alternatively, is the combination of adaptation and induction more effective than either one alone?

A possible mechanism that may play a role is local (retinal) luminance adaptation. To examine other interactions between the sustained and transient components we continuously shifted the phase of the Gabor patch during the adaptation phase of the trial. Drifting the stimulus averages out total local absorbed light energy, and reduces the retinal afterimage. We also examined the effect of reversing the contrast polarity of the adapting and inducing stimuli on the disappearance of the target. This part is discussed in section 3.3.

3.1.1 Methods

The frequency of induced disappearance (8 second adaptation followed by 20ms high-contrast) was compared to the frequency of fading of the target after 8 seconds of adaptation to stationary (1/3 trials) or drifting (2/3 trials) Gabor patch only, and after 20 millisecond high-contrast Gabor. The paradigm is illustrated in Figure 2a,b. The contrast of the Gabor target is 4%, which is considerably above the detection threshold. The null hypothesis is that the probability of failure to detect the target in the combined condition (after adaptation to sustained stimulus followed by transient stimulus) is less than or equal to the sum of the probabilities of detection errors attributable to local peripheral fading (Troxler fading) and forward-masking. Participants were asked to report presence or absence of the target. They could also optionally report if the target partially faded, or appeared like a different pattern such as a Gaussian. Those reports (3.7% of the trials) were discarded from the analysis.

Figure 2 inserted about here

3.1.2 Results and discussion

For parameters used in this experiment, the proportion of detection failure is significantly higher after the combination of the sustained low-contrast adaptation and transient high-contrast induction than either following sustained adaptation or induction alone ($p < 0.00001$, Figure 2c). Furthermore, the disappearance is significantly more frequent than the linear combination of the effects of the two other conditions (26.26% vs. 9.52%, $p < 0.0001$). Hence, induced disappearance can not be explained in terms of Troxler fading or forward masking.

3.2 Experiment 1b

To rule out that observers used different cognitive criteria in Experiment 1a (response bias) we asked five observers (3 naïve plus two authors) to report their confidence in presence or absence of the target. They were informed that the target is absent in half of the trials. Each observer finished two sessions of 48 trials (16 trials per condition). The receiver operating characteristic (ROC-curve) was obtained for each condition (Figure 2d).

3.2.1 Results and discussion

Subjects performed accurately in sustained low-contrast adaptation condition, and nearly as well in brief high-contrast exposure condition (except one subject that confused afterimage of high-contrast Gabor with target). In contrast, participants failed to report the target in the combined condition, even when they were confident about their responses. The ROC-curves suggest that sustained adaptation followed by brief high-contrast induction results both a lower discriminability, and a bias toward failing to report the target. Note that signal detection theory does not have any construct corresponding to subjective awareness of the stimuli (Macmillan & Creelman, 1991). However, the ROC-curve is more compatible with a Gaussian model reflecting low-level detection difficulty (solid line) than a High-threshold model reflecting response bias (High-threshold model predicts ROC-curve would be a straight line) (Wickens, 2002). Furthermore, since the trials were randomized, it is unlikely that observers could switch between different response criteria for different conditions. Thus the obtained differences among the conditions can not be attributed to cognitive or response bias.

3.3 *Phase-sensitivity and retinal component of induced disappearance*

The results in Experiment 1a were examined for any effect of contrast-polarity. Figure 3a compares induced disappearance following sustained adaptation to stationary vs. drifting Gabor signal (phase shifted by $\pi/2$ every 250 milliseconds). Probability of disappearance was significantly higher following adaptation to drifting Gabor signals compared with the stationary signals ($p < 0.001$). For the stationary condition, the frequency of disappearance after adaptation to stationary Gabor was not affected by reversing its polarity with respect to the target same phase vs. opposite-phase ($p = 0.89$).

We also looked for any effect of the polarity of the high-contrast inducer with respect to the target, using drifting contrast during the sustained adaptation (Figure 3b). The detection was not found to be affected by the polarity of the transient high-contrast Gabor, either ($p > 0.4$).

Neurophysiological evidence indicates that the early representation of visual information (retina, LGN, V1 simple cells) is selective for spatial phase information, but higher areas lose their selectivity. Our results suggest that phase-invariant cortical mechanisms are involved for both adaptation and induction phases of induced disappearance.

Figure 3 inserted about here

3.4 *Experiment 1c: Induced disappearance as a function of adaptation time*

Based on the above results (Figure 2c,d) we argue that induced disappearance can not be explained as fading by visual transients (Kanai & Kamitani, 2003). First, blinking of the sustained low-contrast Gabor alone for 50ms (Figure 2a) does not induce disappearance of the target. Second, adaptation appears to be a necessary component (in contrast to Kanai & Kamitani's remark that prolonged adaptation is not necessary).

The cumulative nature of the adaptation in induced disappearance can be best illustrated by varying its duration (Figure 4). The duration of sustained adaptation (drifting Gabor) was varied between 0 (no adaptation) to 14 seconds in 4 participants. A 20ms high-contrast inducer followed adaptation. Half of the

trials were conducted without flashing the high-contrast pattern (no induction) and served as control (dotted line).

For both induced disappearance and control conditions the probability of failing to detect the target increases almost monotonically as a function of adaptation time, suggesting temporal integration. For the combined condition the effect starts earlier and rises faster as the duration of adaptation increases compared with the control (adaptation only) condition, indicating synergy between adaptation and induction.

Figure 4 inserted about here

4 Ocular transfer

4.1 *Experiment 2*

We examined ocular transfer of induced disappearance using dichoptic stimulation. Observers viewed the monitor through a set of mirrors, such that each eye viewed a separate region of the screen. Adapting low-contrast and brief high-contrast stimuli were presented to one eye. In 40% of the trials, the target was presented to the same eye. In another 40%, the target was presented to the other eye. The target was absent in the rest of the trials. Participants were asked to report if the target is absence or presence. Each participant ran 30 trials.

4.1.1 Results

In the monoptic condition (where adapting and test stimuli were presented to the same eye), participants failed to report the target in $35 \pm 6.2\%$ of the trials (mean \pm SEM), whereas in the dichoptic condition (target was presented to the eye that was not adapted), in $31.7 \pm 6\%$ of the trials observers reported target presence as absence. Although the effect is slightly stronger in the former condition, the difference was not significant ($p=0.81$). We conclude that the site of adaptation is cortical, consistent with results from Experiment 1.

5 Orientation selectivity

5.1 Experiment 3

The disappearance of the target in Experiments 1 and 2 does not necessarily indicate suppression of neural activity due to adaptation, as we have suggested. Higher-level mechanisms such as attention (as opposed to specific mechanisms) underlie similar illusions in which an otherwise salient stimulus is not perceptually resolved. For example, in attentional blink paradigm observers are not aware of a target presented in a time window around some non-specific distracting event. Similarly, in crowding phenomena (He, Cavanagh & Intriligator, 1996), the observer is unable to resolve the orientation of the target (although strictly speaking the target is not invisible in this case).

One way to dissociate higher-level and low-level mechanisms is to look at the orientation selectivity of the effect. Adaptation is selective for orientation, at least in early stages of the human visual hierarchy. Result of a preliminary experiment in our lab indicated that sustained adaptation to a Gabor pattern has little effect on the detection threshold for orthogonal orientation. However, a general mechanism such as spatial attention or location-based inhibition of return does not depend on the orientation of the preceding stimuli. Consequently, positive evidence for orientation specificity could imply involvement of low or intermediate level visual mechanisms, namely, adaptation.

5.1.1 Methods

We compared disappearance induced by high-contrast patterns with same or orthogonal orientation to the target pattern (Figure 5a-d). Induction followed 4 or 8 seconds of adaptation.

5.1.2 Results and discussion

Detection of the target subsequent to adaptation was found to be highly selective for the orientation of the sustained low-contrast stimulus ($p < 0.0001$, after both 4 and 8 seconds). There was hardly any disappearance when observers were adapted to a Gabor patch orthogonal to the test (Figure 5c).

Induced disappearance was partially selective for the orientation of the high-contrast inducer. Although there was some effect when inducer had orthogonal orientation (Figure 5b), the frequency of disappearance

was considerably reduced ($p=0.054$ and 0.016 after 4 and 8 seconds, respectively). Therefore, induced disappearance involves orientation specific adaptation.

Although all adapting stimuli have the same texture boundaries, disappearance occurs only when the adapting texture has the same orientation as the target. It indicates that the adaptation to texture boundaries does not underlie induced disappearance. The results suggest involvement of early or intermediate visual processes in induced disappearance. High-level mechanisms lacking orientation selective representations can not exclusively mediate the effect.

Figure 5 inserted about here

6 Spatial and Contextual Effects

Adaptation can be specific to the region that the stimuli were presented (as in retinal light adaptation), or it can extend into other parts of the visual field. Non-local effects indicate lateral connections within early cortical areas or secondary mechanisms and involvement of intermediate or high-level areas. Such mechanisms might be affected by grouping and other contextual effects.

In preliminary experiments, we failed to induce disappearance at locations other than where it was adapted to sustained stimulus. In contrast, disappearance could be induced by briefly flashing a high-contrast Gabor in the 2-3 degree vicinity of the adapted location. Induction in the opposite hemi-field had no effect. These findings are comparable to high orientation-selectivity for sustained low-contrast and partial selectivity for transient high-contrast induction in Experiment 3. In experiments 4a and 4b we investigated if a) induction simply depends on distance, and b) there is any contextual effect.

6.1 *Experiment 4a*

In order to determine whether induced disappearance is a local (location specific) effect or not, a large low-contrast drifting Gabor signal ($\sigma= 2$ deg) was presented on the screen during the adaptation phase (8 sec), followed by either a small ($\sigma= 1.2$ deg) or large ($\sigma= 2$ deg) high-contrast Gabor (20ms). The target

was always a large ($\sigma = 2$ deg) Gabor signal. Subjects were asked to press one out of five keys to report what they perceived (a)Large Gabor, (b)small Gabor, (c)ring, (d)parallel lines, or (e)nothing (i.e. complete fading). The paradigm and results are presented in Figure 6.

6.1.1 Results and discussion

Observers experienced complete disappearance of the target more frequently after induction by the larger stimulus than the small one. Partial and incomplete fading of the target were reported more commonly following the small inducer. These results suggest that the size of the transient inducer affects the disappearance of the subsequent target. Nonetheless, the dominant pattern of the incomplete fading is the disappearance of the periphery of the target, which contradicts a purely local effect because only the central portion of the target overlaps the inducer. Observers did not perceive the target as a hollow ring (“Local Fading” in Figure 6) in the small inducer condition - which is predicted by the local adaptation - more frequently than when the larger inducer was used ($p > 0.7$).

Figure 6 inserted about here

6.2 Experiment 4b

Experiment 4a demonstrates that a transient high-contrast pattern smaller than the target fails to induce a perceivable local disappearance. However, filling-in with the peripheral part of the Gabor pattern may confound the results by masking a small local scotoma. To rule out this explanation and study the possibility of contextual effects, we introduced two separate Gabor signals ($\sigma = 1.4$ deg, center to center distance = 3deg, Figure 7a,b). During the adaptation phase, both locations experience adaptation to the low-contrast drifting Gabor. The Gabor patches were oriented either parallel (or collinear), or orthogonal to each other. A high-contrast signal with the same orientation was briefly displayed for 20 ms at one of the locations (e.g., location 1). Participants were asked to report presence or absence of subsequent low-contrast targets at both locations by pressing two keys in succession (two 2-AFC tasks). If disappearance is a local effect, observers should experience disappearance only at location 1. On the other hand, if induced

disappearance involves global mechanisms, one might experience disappearance at both locations, and particularly at location 2. In 27% of the trials, one or both targets were absent (not included in the analysis).

6.2.1 Results and discussion

The results are illustrated in Figure 7c. Each bar depicts proportion of trials that observers failed to report both (white bars) or one (gray and black bars) of the two targets. The pattern of responses was different for condition a (same orientation, Figure 7a) and b (orthogonal orientation, Figure 7b) ($p < 0.001$). In condition a (left three bars), observers reported both target as absent in 16% of the trials. In another 15% of the trials, they only failed to report the target at location 1 (same as induction). In 7% of the trials, target 1 was detected, but participants failed to detect target 2 (no induction at location 2). Overall, in 41% of all trials that disappearance was induced, disappearance was induced in both locations. In condition b, disappearance was more isolated to one location. Only in 21% of trials with disappearance, it was reported in both locations (a vs. b: $p < 0.001$).

Results confirm that induction is carried out by non-local mechanisms. In more than 22% of the trials subjects failed to detect the target located where induction had not taken place (location 2), which considerably higher than 5% of trials in Experiment 1a for low-contrast adaptation only. We already mentioned that induced disappearance does not transfer following eye-movement. This is not inconsistent with the transfer in Experiment 4b because retinal-motion signal is absent in Experiment 4, and the effect transfers to a previously low-contrast-adapted location (rather than an unadapted retinal area following eye-movement). Nonetheless, the original target (the same location as the induction) still undergoes disappearance more frequently than the alternative target, indicating that although the effect is not purely local, proximity still plays some role.

Figure 7 inserted about here

Experiment 3 demonstrates that induced disappearance has orientation selective components. Experiment 4b suggests that it might also spread in an orientation selective manner, either because the underlying mechanisms is orientation-selective, or because co-linear Gabor patches tend to perceptually

group together more often than orthogonal Gabor patches. As mentioned above, when the targets are collinear or parallel, they tend to disappear together, indicating that disappearance obeys perceptual grouping. The overall frequency of the disappearance of the target at the location of the transient is not significantly different between the two conditions, and is similar to the results in Experiments 1a. That is, the presence of another stimulus does not weaken the induced disappearance. Notably, the target disappears slightly more often when the other location is adapted to a Gabor patch with orthogonal orientation (35.5 percent vs. 30 percent, $p=0.23$, N.S.). It is also worth mentioning that in some of the trials subjects could detect the target that followed the transient, but failed to detect the target at location 2, as if the disappearance is induced in the first place and then is transferred to the other location.

7 General Discussion

7.1 Summary

In Experiments 1-4, we studied the effect of adaptation on the detection of peripheral low-contrast Gabor patches by using the following paradigm: a low-contrast Gabor patch was presented for several seconds, and then was briefly replaced by a high-contrast patch. Afterwards, subjects were presented with a low-contrast Gabor patch or homogenous background, and were asked to report their percept. In a significant number of trials subjects failed to detect the presence of the target. Both sustained adaptation to the low-contrast stimuli and induction of disappearance by the transient high-contrast stimuli were necessary to get this effect. The target was otherwise easily detectable. Subjects failed to detect the target more frequently when the retinal adaptation during the presentation of the sustained stimulus was minimized by slowly drifting the phase of the Gabor patch than when stationary Gabor patches were used for sustained adaptation. On the other hand, adapting to orthogonal orientations reduced or even eliminated the effect.

Thus, in many of the trials the target stimulus was not consciously registered. Observers failed to detect it either as a consequence of earlier sensory suppression, or alternatively as a result of later removal of the signals by a high-level process. Sensory suppression is often conceived as a mechanism that keeps stimuli from reaching visual awareness by affecting the afferent pathway to the cortex or the cortex itself (Blake, 1989; Burbeck & Kelly, 1984). Although a pre-cortical component has been suggested for suppression in

Troxler fading (Goldstein, 1974; Kotulak & Schor, 1986), we ruled out retinal and pre-cortical adaptation by demonstrating that; (a) detection probability does not depend on the contrast polarity of the stationary stimuli (Experiment 1a), and (b) a substantial degree of interocular transfer occurs (Experiment 2) . These findings imply that the adaptation component responsible for the current effect occurs at or after complex cells in V1 since opposite contrast polarities are conveyed by different and independent channels in retina and LGN that are not affected by adaptation of the other.

7.2 *Induced disappearance and optimal coding of contrast*

Suppression following adaptation can be modeled by a threshold non-linearity: sustained and transient stimuli both locally increase the threshold, and the results are qualitatively explained in terms of linear summation (or temporal integration) of the threshold increments. Nonetheless, this naïve scheme hardly accounts for the magnitude of the effect of a transient high-contrast stimulus as brief as 20-30 ms. Different selectivity for orientation and location also indicates that sustained and transient stimuli play distinct roles.

Adaptation is viewed as a mechanism that dynamically adjusts the mapping between the range of stimulus intensities and the neural codes (Attneave, 1964; Wainwright, 1999; Brenner, Bialek & de Ruyter van Steveninck, 2000). This view can help understanding the illusion. Assume that the mapping (alternatively the psychometric curve) is monotonic in form of $f(\text{input}/\text{gain} - \text{offset})$, where f is the standard normal cumulative distribution function, and gain reflects the standard deviation of the input, and the observer has some inherent internal noise which is independent of the input. Discriminability of two levels of stimulus intensity is inversely proportional to the slope of f at those values. For efficient coding (in statistical sense), discriminability should be high for events that occur with high frequency, and low for low-frequency events. That is, the mapping (offset , gain) should conform to the distribution (mean, variance) of the inputs (Figure 8). As the distribution is not a priori fixed, the ideal observer should estimate and dynamically update distribution parameters. As a side-effect of this process, adaptation followed by induction might affect the gain and offset in a way that renders a subsequent low-contrast target sub-threshold.

The likelihood of a particular distribution can be estimated from the input using Bayesian inference. The posterior probability is proportional to the probability of the data given the distribution times the prior

probability of the distribution. For inputs around the mean (where probability of the data given the distribution is around its maximum), the likelihood changes gradually. Consequently, estimation of the optimal offset for neural code requires temporal integration (deWeese & Zador, 1998; Fairhall et al., 2001). In contrast, a sudden increase in the range of stimulus intensities dramatically alters posterior probabilities and rapidly modulates the gain (deWeese & Zador, 1998; Fairhall, Lewen, Bialek & de Ruyter Van Steveninck, 2001). In this framework, we propose that sustained low-contrast adaptation gradually increases the offset and the gain, elevating the detection threshold. Then, induction reduces the gain without effectively affecting the offset, resulting target contrast to fall below the range of intensities encoded effectively by neurons, as schematically illustrated in Figure 8. The model can explain induced disappearance and is consistent with electrophysiological data (Ohzawa, Sclar & Freeman, 1985) and psychophysical experiments that showed that detection threshold (which reflects offset) but not discrimination threshold (which reflects gain) increase after prolonged adaptation to low-contrast stimuli (Maattanen & Koenderink, 1991)¹.

Figure 8 inserted about here

7.3 *Neural mechanisms involved in induced-disappearance*

In terms of neural circuitry, suppression by transient stimulus involves either inhibitory feedbacks from higher-level areas or suppression within the early visual cortices. Induced disappearance cannot be explained by cross-orthogonal suppression (because effect disappears after adaptation to orthogonal stimulus) or inter-ocular suppression (because monoptic and dichoptic adaptation are similarly effective) within primary visual cortex. Both cross-orthogonal and inter-ocular suppression are reportedly stronger or equal between orthogonal stimuli than stimuli with the same orientations (Benevento, Creutzfeldt & Kuhnt,

¹ Note that our distinction between offset and mean is arbitrary. However, offset reflects the highest level of stimulus intensity that should be ignored, whereas mean reflects intensities with highest discriminability. In this interpretation, adaptation seems to adjust offset rather than mean.

1972; Blakemore & Tobin, 1972; Freeman, Durand, Kiper & Carandini, 2002; Sengpiel & Blakemore, 1994; Sengpiel, Freeman & Blakemore, 1995). In contrast to monocular rivalry (Campbell, Glinsky, Howel, Riggs & Atkinson 1973), disappearance is weakened following exposure to patterns orthogonal to the target. In short, suppression does not seem to be posed by known inhibitory connections within primary visual cortex.

In Experiment 4b we presented two sustained low-contrast adaptation stimuli and two targets, but the transient high-contrast inducer only appeared at one location. In a substantial number of trials subjects failed to detect the target at the other location or both targets disappear at the same time. Co-linear targets disappeared together more frequently than orthogonal targets, consistent with mechanisms that involve perceptual grouping and contextual effects. Similar results have also been reported in other disappearance illusions. Disappearance might be induced by stimulating a location other than the targets in fading induced by visual transients (Kanai & Kamitani, 2003) and motion-induced blindness (Bonneh et al., 2001). Perceptual grouping effects are also observed for motion-induced blindness (Bonneh et al., 2001). These findings are in agreement with the view that target disappears as a result of an active process that involves higher-level selection mechanisms (Logothetis, 1998; MacKay, 1986). There is evidence of involvement of fronto-parietal areas in altering or modulating the percept in related illusions such as motion-induced blindness (Pettigrew & Carter, 2002), binocular rivalry (Lumer, Friston & Rees, 1998), and crowding phenomena (Afraz, Montaser-Kouhsari, Vaziri-Pashkam & Moradi, 2003). It is plausible that the same brain regions be involved in, or modulate, induced disappearance.

Although the results of Experiment 4 and other evidence appear to indicate involvement of extra-striate processes, explanations based solely on non-specific mechanisms such as the limitation of attentional resources or filling-in induced by secondary (texture defined) edge adaptation are not consistent with our results and can not explain the orientation-specificity of the effect. We failed to induce disappearance by flashing the high-contrast inducer in the opposite visual field, i.e., by covertly shifting attention away from the target. In induced disappearance, both sustained adaptation and transient high-contrast are necessary to induce the effect. Attentional resources at the time that target is presented should not be affected by previous adaptation. There is also little evidence about the dependence of other related mechanisms such as change-blindness and inhibition of return to the previous history of adaptation to some specific orientation.

This is not to say that attention can not modulate the effect. Attention plays a role in peripheral fading (Lou, 1999) and might also affect the performance of the subject in induced disappearance, presumably by increasing the exposure of the neural circuitry that undergoes adaptation to the adapting stimulus. However, taken all together, our results put the underlying mechanism at the interplay between intermediate and early cortical levels of visual processing.

7.4 *Conclusion*

We dissociated between sustained adaptation to a low-contrast spatial pattern and transient induction with a high-contrast stimulus and demonstrated a combinatory effect that indicates synergy between contrast and adaptation. A phenomenological model that can explain the results in terms of contrast gain and offset was presented based on the idea of optimal neural encoder (Attneave, 1954). Results establish cortical origins for both sites of transient and sustained adaptations involved in induced-disappearance phenomenon. The effect is selective for orientation. Furthermore, it was established that the disappearance of the target involves non-local mechanisms, conceivably associated with top-down influence and contextual modulation. Considering the similar characteristics in a wide variety of experimental manipulations, the same mechanisms may also underlie suppression of object boundaries in illusions such as motion-induced blindness or fading induced by visual transient.

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9 Figure Captions

Figure 1. a,b) Induction of disappearance by brief presentation of a high-contrast stimulus after adaptation to a low-contrast pattern. c) Reversing the order of the sequence removes the effect.

Figure 2. Induction of disappearance by brief presentation of high-contrast Gabor after adaptation to low-contrast stimulus a,b) the experiment paradigm (a: low-contrast alone, b: low-contrast followed by high-contrast, high-contrast alone condition is not shown). c) results for nine subjects. d) ROC-curves for five subjects, same conditions as in c.

Figure 3. a) Disappearance after sustained adaptation to stationary or drifting low-contrast Gabor for eight seconds, followed by transient induction by high-contrast Gabor (nine subjects, same as Figure 2a-c). The stationary low-contrast sustained adaptation had either the same polarity as the target or the opposite polarity. There is no significant effect of contrast polarity for stationary adaptation. In the drifting condition the phase of the Gabor patch was shifted by $\pi/2$ every 250ms to minimize retinal adaptation during the sustained adaptation. This appeared as a slow and relatively smooth motion to the subjects. b) Effect of contrast polarity of the high-contrast stimulus (with respect to the target) on induction of disappearance. Same subjects and same experiment as Figure 2a-c. High-contrast Gabor patch followed eight seconds of adaptation to a drifting low-contrast stimulus. Error bars indicate S.E.M.

Figure 4. The effect of the duration of sustained adaptation to low-contrast Gabor signal followed by induction by brief presentation of high-contrast Gabor on detection of the subsequent target (solid line), compared with adaptation to low-contrast alone (dashed line) (four subjects, pooled data). Error bars indicate S.E.M.

Figure 5. Orientation selectivity of the flash induced disappearance. The experiment paradigm is depicted on the left side. a) induction using high-contrast Gabor with the same orientation as the low-contrast stimuli, b) high-contrast induction with orthogonal orientation to the low-contrast stimuli (adaptation and target), c) sustained adaptation to low-contrast Gabor with orthogonal orientation with the target, induction with same orientation as target, d) low-contrast adaptation without induction with high-contrast (control), e) results: A vs B: $p > 0.05$ after 4 sec, $p = 0.016$ after 8 sec, B vs. D, $p < .01$, after 4 sec, $p < .0001$ after 8 sec (10 subjects).

Figure 6. Disappearance following local induction. There is no significant difference between the responses of observers for trials with small inducer compared with trials with larger inducer ($\chi^2 = 4.1095$, $df = 4$, $p > 0.35$, 4 participants). Participants had to report if they perceived the target or not (complete fading), and if the target was perceived as a smaller Gabor patch (peripheral fading, an illustration was shown in the inset of the graph), as a hollow ring (local fading), or anything else (partial fading).

Figure 7. Disappearance subsequent to induction by high-contrast Gabor at one of the two neighbor target locations. The two targets are either (a) collinear or (b) orthogonal to each other. The transient stimulus (induction) appears only at one of the two locations. c) Disappearance is observed in both locations. The effect depends on the orientation similarity between the two locations (six subjects. $p < 0.001$, $\chi^2 = 16.65$, $df = 3$). In some trials, subjects failed to detect any of the two targets. In other trials, subjects failed to detect only one of the targets, which was not always consistent with the location of the transient (same vs. other location).

Figure 8. The hypothetical stimulus-response curve for neurons and its modulation after adaptation. a) the stimulus-response curve before adaptation. This curve is optimal for intensities around m_1 (indicated by a small arrow above the graph). However, this curve is not optimal for stimulus intensities around m_2 , and the response for x is saturated. b) adaptation may improve coding efficacy by modulating the offset (threshold) of the stimulus-response curve in the case that the mean input intensity is m_2 (given a constant variance), or by reducing the gain (slope) when the mean is m_1 but some samples are as high as x (increased variance). These conditions respectively correspond to sustained adaptation to low-contrast vs. induction (adaptation to high-contrast). Notably, modulation of both offset and gain has a combinatory effect, resulting m_2 to fall below the threshold. c) Biological plausibility: the input current vs. firing rate curve for a leaky integrate-and-fire model neuron with refractory period. Shunting-inhibition elevates the offset, where as increasing the spike-threshold (via a hyperpolarizing current) modulates the gain. Again, there is a large combinatory effect when both gain and offset change.

10 Figures

Figure 1

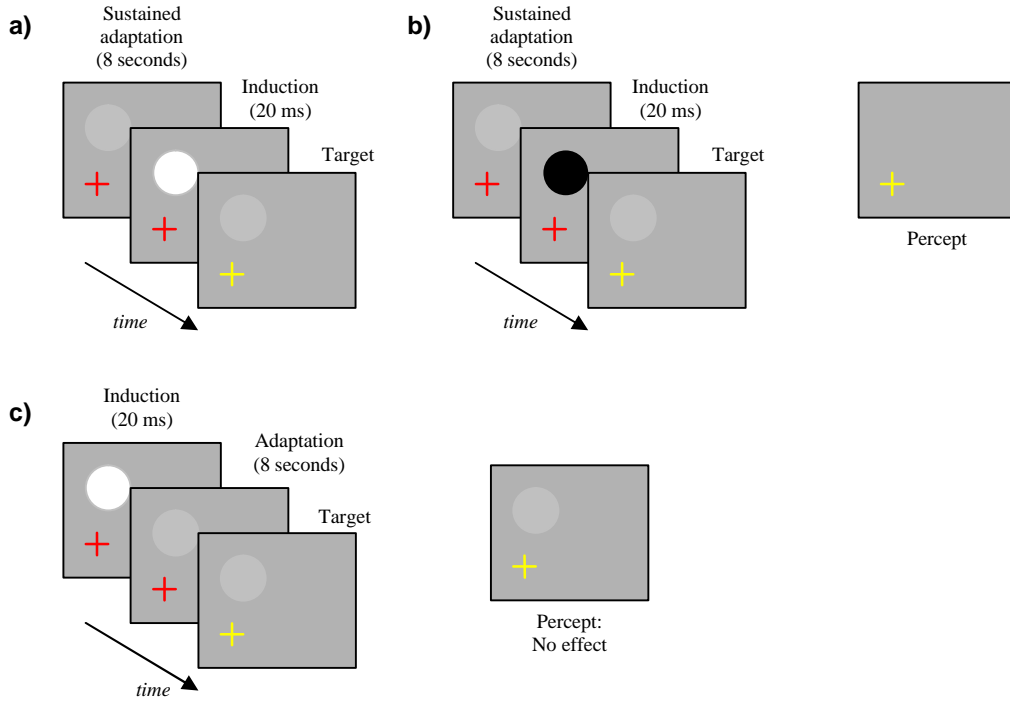
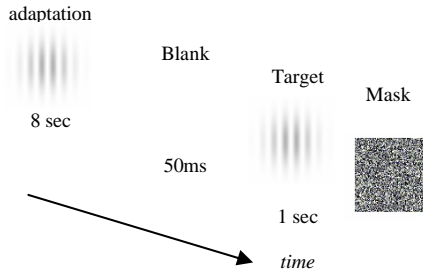
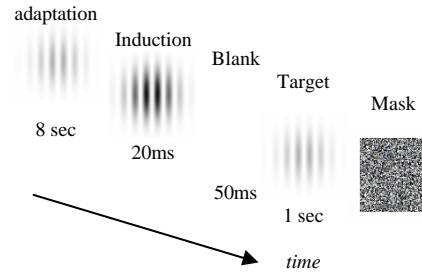


Figure 2

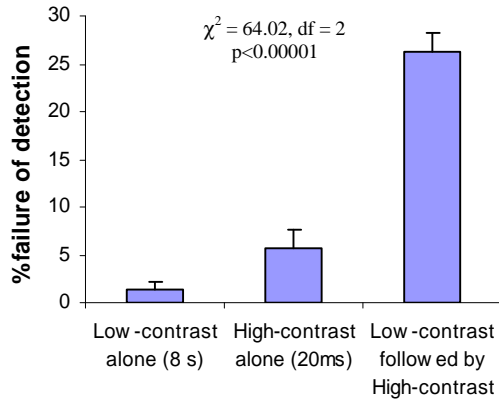
a) low-contrast alone



b) low-contrast followed by high-contrast



c)



d)

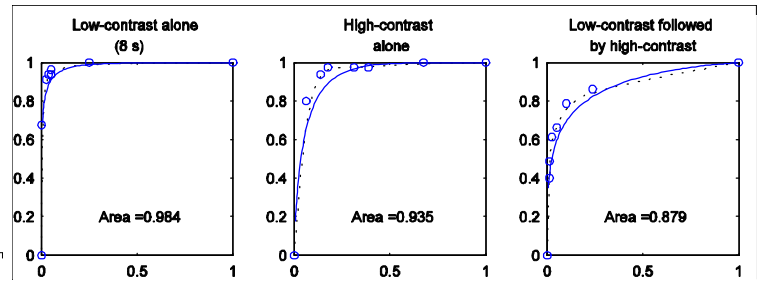
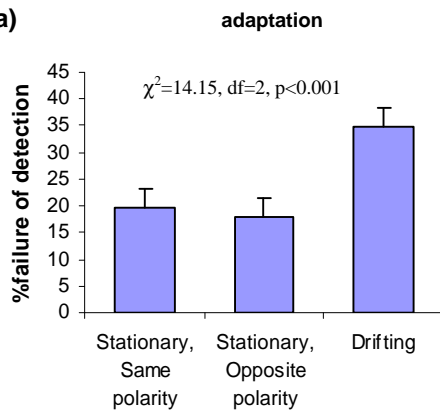


Figure 3

a)



b)

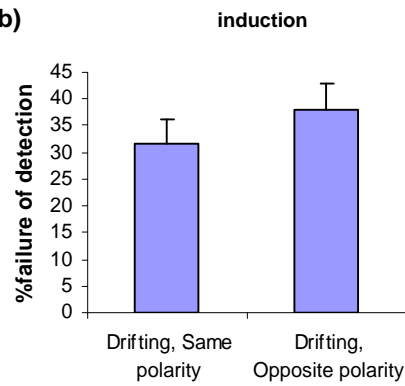


Figure 4

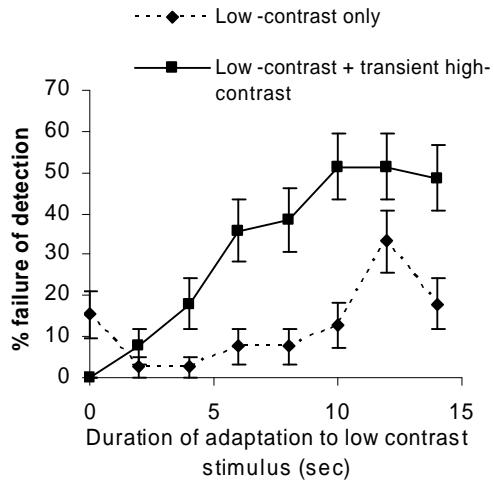


Figure 5

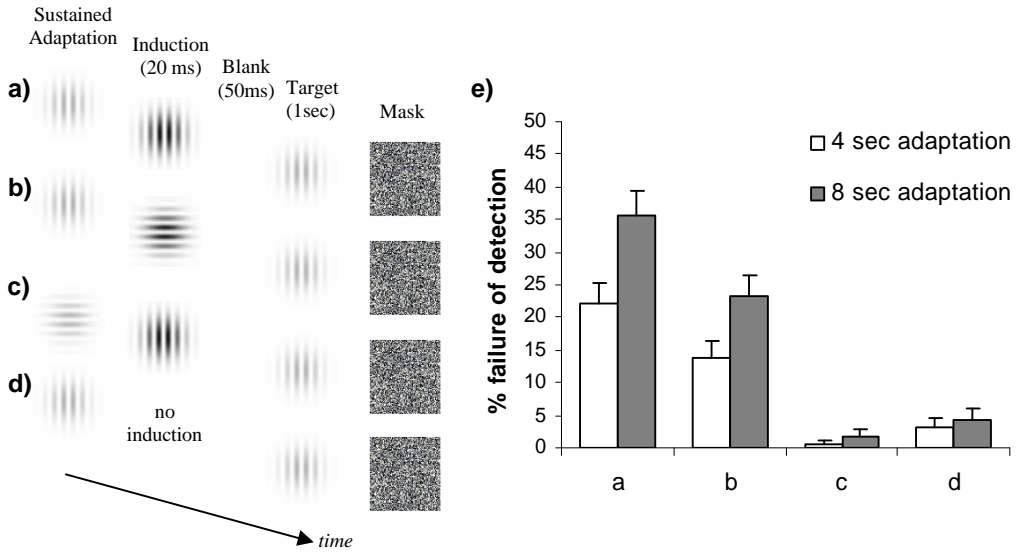


Figure 6

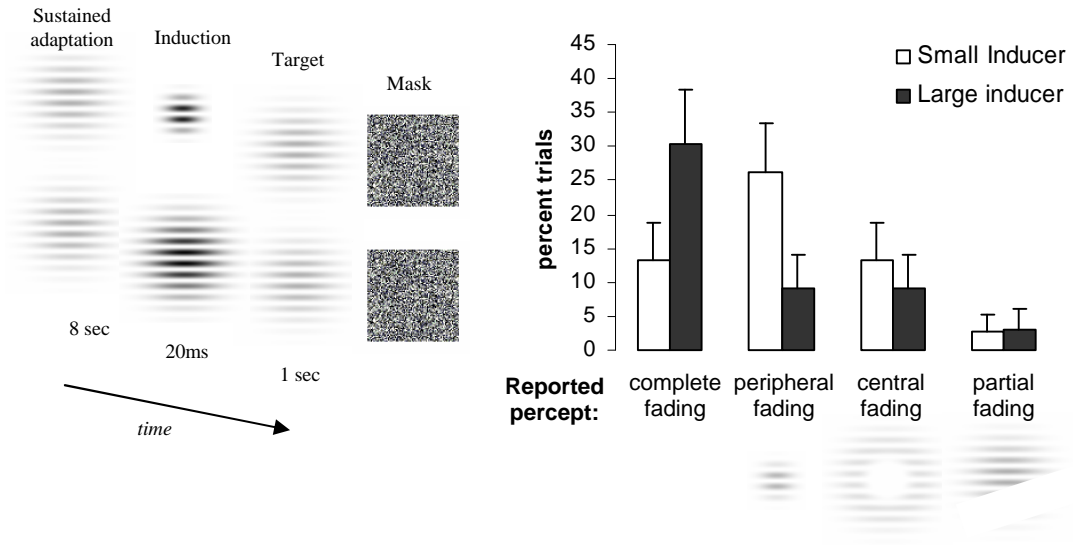


Figure 7

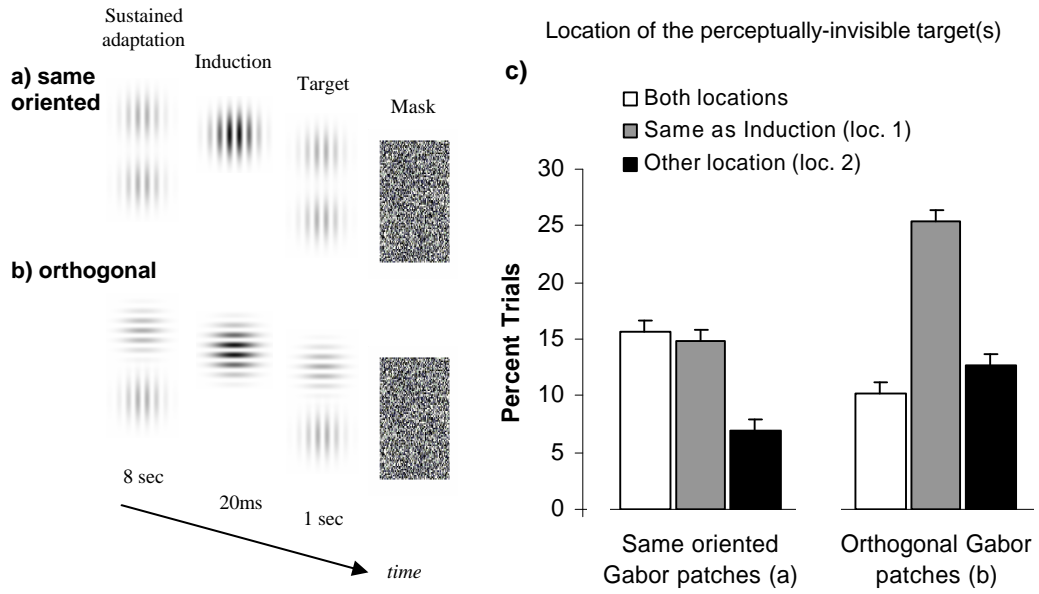


Figure 8

